



# A NEW PRIMITIVE TETRAPOD, *WHATCHEERIA DELTAE*, FROM THE LOWER CARBONIFEROUS OF IOWA

by R. ERIC LOMBARD *and* JOHN R. BOLT

**ABSTRACT.** *Whatcheeria deltae* gen. et sp. nov. is Viséan V3b in age and is represented by the second oldest tetrapod skeletal remains so far described from the Americas exclusive of Greenland. *Whatcheeria* is a primitive tetrapod about 1 m in length including the tail, and is characterized by the following autapomorphies: ornament on cranial dermal bones is absent or extremely light; the parietal foramen is large relative to skull size; the prefrontal forms a thick, raised ridge at the anterodorsal margin of the orbit; and the cleithrum terminates posterodorsally in a robust, posteriorly directed process above a deep notch. *Whatcheeria* is extremely plesiomorphic in retaining: a cheek with long postoccipital portion; a preopercular; lateral line canals that in places are completely encased in bone; a dentary which extends far posteriorly along the adductor fossa; a prearticular that extends anteriorly almost to the symphysis; a toothed adsymphysial; a row of small Meckelian foramina between the prearticular and infradentary bones; a tabular and parietal that are not in contact; a nearly continuous row of teeth on the vomer, palatine and ectopterygoid; a femur with an oblique ridge having a maximum elevation at midshaft; and a pelvis with an area of unfinished bone anterior to the acetabulum.

The phylogenetic affinities of *Whatcheeria* are uncertain at present, but its best placement may be as the first outgroup to the Anthracosauria *sensu* Gauthier *et al.* 1988. This suggestion is supported by the presence of: small post-temporal fenestrae; a tabular horn that continues from the dorsal surface of the tabular; a skull table in which the temporal bones have a strong ventral inflection dorsal to their sutures with the cheek; dermal ornament that, though generally absent, where present is similar to the 'anthracosaur type'; quadrangular orbits; narrow vomers; marginal fangs on the maxilla; an interclavicle with a long parasternal process; and a scapulocoracoid that ossifies from two centres. In the context of this hypothesis of relationships, some of *Whatcheeria*'s observed features are unexpected: pleurocentra that are sometimes composed of dorsally fused antimeres; a region of presacral ribs with flattened shafts and large uncinat processes; and absence of an ossified branchial skeleton.

THE earliest tetrapod remains that can be securely dated come from the Late Devonian, and their very primitive nature suggests that tetrapod origins did not much antedate this time. Eight tetrapod genera represented by skeletal remains have been described from six Devonian localities, in Australia, East Greenland, Russia, Latvia, Pennsylvania and Scotland (Säve-Söderberg 1932; Jarvik 1952; Campbell and Bell 1977; Lebedev 1984; Ahlberg 1994, 1995; Daeschler *et al.* 1994). Lower Carboniferous tetrapods are nearly as rare. Nineteen published localities have produced skeletal remains of about that number of tetrapod genera (Romer 1969; Carroll *et al.* 1972; Smithson 1982, 1985a; Bolt *et al.* 1988; Schultze and Bolt in press). Most of these Devonian and Lower Carboniferous tetrapods are represented by few and/or poorly preserved specimens. Notable exceptions are *Ichthyostega* and *Acanthostega* from the Devonian of East Greenland, and *Greererpeton* from the Lower Carboniferous of Greer, West Virginia, USA. These three genera have provided much of the information upon which our present understanding of the earliest tetrapods rests (Jarvik 1980; Smithson 1982; Clack 1988, 1989, 1994a, b; Godfrey 1989; Coates and Clack 1990, 1991; Clack and Coates 1993).

Four of the Lower Carboniferous tetrapod-producing localities were discovered relatively recently: Dora Open Cast site (= Cowdenbeath), Scotland (Andrews *et al.* 1977); East Kirkton,

Scotland (Wood *et al.* 1985); Goreville, Illinois, USA (Schultze and Bolt in press); and Delta, Iowa, USA (Bolt *et al.* 1988). These localities are important because of their age, the number and quality of specimens produced, and the opportunity they present to collect and prepare early tetrapod specimens with the aid of modern techniques and equipment. Indeed, specimens from these sites have now begun to provide new insights into early tetrapod evolution and will do so for years to come (Wood *et al.* 1985; Milner *et al.* 1986; Smithson 1989, 1994; Bolt 1990; Rolfe *et al.* 1990; Smithson and Rolfe 1990; Clack 1994c; Milner and Sequeira 1994; Smithson *et al.* 1994; Schultze and Bolt in press). We here name and describe briefly a new tetrapod that is represented by numerous and often excellently preserved specimens from the Delta, Iowa locality.

#### LOCALITY AND HORIZON

The Delta locality consists of two adjacent palaeodepressions or collapse structures, exposed in the walls of an inactive limestone quarry. The quarry is in the upper part of a rock unit which has traditionally been referred to as the St Louis Formation (Bolt *et al.* 1988). Studies by members of the Iowa Geological Survey Bureau suggest, however, that only the lower portion of the Iowa 'St Louis Formation' is correlated with the type section of the St Louis Formation, near the Missouri city of that name. The upper part of the Iowa 'St Louis' may correlate instead with the Ste Genevieve Formation (eastern Missouri and western Illinois).

The collapse structures at the Delta site are believed to have developed within the Waugh and Verdi members of the Iowa 'St Louis Formation' during Waugh time (Witzke *et al.* 1990). The Verdi Member records the offlap of an epicontinental sea. The sandstones, shales, and lime mudstones that constitute the overlying Waugh Member lack a definitively marine invertebrate fauna. The Iowa Geological Survey Bureau interprets the depositional environment of the Waugh Member as 'lacustrine, fluvial, and swamp environments in a coastal lowland setting' (Witzke *et al.* 1990, p. 45). The environment of the tetrapod-producing layers within the collapse structures (Units C and D of Bolt *et al.* 1988 and Witzke *et al.* 1990) is interpreted similarly. Thus it is considered to have been primarily lacustrine, fresh-water to brackish, with possible intermittent incursion of marine waters.

In the absence of a normal marine fauna, the age of the Waugh Member has been determined by 'bracketing' it between the Verdi Member of the 'St Louis Formation,' which directly underlies it, and the Pella Formation. The Pella Formation generally overlies the Waugh Member of the 'St Louis Formation' in this area of Iowa, but has been removed erosionally at the Delta site. Foraminiferal and conodont data suggest an age of Viséan V3b for the Verdi Member, and upper V3b to lower V3c for the Pella Formation (Witzke *et al.* 1990; R. M. McKay, pers. comm. 1993). The most probable age for the Delta collapse-structure fills is thus Viséan V3b, i.e. Asbian, c. 340 Ma.

Most of the Delta sink fills have now been excavated, mainly during 1986 and 1988. Over 600 tetrapod specimens were recovered, including about 50 partial skeletons, some nearly complete,

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#### EXPLANATION OF PLATE I

*Whatcheeria deltae* gen. et sp. nov., FM PR 1700, type specimen. Skull in association with pre-sacral vertebral column, partial shoulder girdle, ribs, and partial hindlimb. Skull is in dorsal view, with right cheek and lower jaw visible, left cheek and lower jaw folded under. Note large parietal foramen, and maxillary fangs on both sides; premaxillary fangs are buried in matrix. On the left side of the specimen, a clavicular stem protrudes directly laterally at midlength of the preserved vertebral series; opposite this, on the specimen's right side, the interclavicle and its stem are partly visible, separated by a break. Right femur, tibia and fibula are seen in flexor view on the specimen's right side. Phalanges are visible at posterior end of vertebral series. Scale bar represents 50 mm.



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along with several hundred fish and some invertebrate and plant fossils. All specimens are in the collections of the Field Museum of Natural History and the University of Iowa. Delta fossils are generally well-preserved, and most retain excellent surface and internal detail, even though many have been crushed. The tetrapod described here is by far the most abundant taxon, and may prove to constitute some 90 per cent. of tetrapod specimens. At least two other tetrapods are present in addition: an embolomere, and a colosteid temnospondyl. Both are apparently new. The fish fauna includes the lungfish *Tranodis* (Schultze and Bolt in press), osteolepiform crossopterygians (a rhizodontid and an osteolepidid), acanthodians, elasmobranchs, palaeoniscoids, and the ichthyolith *Cynopodius*.

The description presented here will be expanded when preparation is nearer completion. Approximately 200 specimens of Delta tetrapods have been completely or nearly completely prepared to date, but much remains to be done.

Institutional abbreviations used in this paper are: FM, Field Museum of Natural History; SUI, University of Iowa.

## SYSTEMATIC PALAEOLOGY

TETRAPODA *sensu* Gaffney 1979

CLASS, ORDER and FAMILY undesignated

GENUS *Whatcheeria* gen. nov.

*Derivation of name.* From the town of What Cheer, Iowa, USA, home of the discoverer of the Delta tetrapods, Mr M. P. McAdams.

*Whatcheeria deltae* sp. nov.

Plate 1; Text-figures 1–9

*Holotype.* FM PR 1700, skull in association with pre-sacral vertebral column, partial shoulder girdle, ribs, and partial hindlimb (Pl. 1).

*Referred and Cited Specimens.* FM PR 1634 (Text-fig. 1): skull with lower jaws, nearly complete though crushed; atlas, axis, and several additional anterior vertebrae and ribs; part of dermal shoulder girdle. FM PR 1635: skull with lower jaws, articulated partial vertebral column, two scapulocoracoids, humerus (Text-fig. 7B), radius and ulna, plus other appendicular elements; all severely crushed. FM PR 1636: partial skull with several crushed and disarticulated vertebrae. FM PR 1644: block with right and left lower jaw, clavicle, rib, and other elements. FM PR 1651: skull table with frontals, postfrontals, dorsal and ventral sides prepared free. FM PR 1652: partial skull roof with frontals broken off and area around parietal foramen broken out; crushed and incomplete otic capsules present; braincase and both stapes crushed up onto underside of skull roof. FM PR 1701: braincase associated with first three vertebrae. FM PR 1704: left scapulocoracoid with cleithrum. FM PR 1712 (Text-fig. 4): two isolated pleurocentra. FM PR 1740: right half of pelvis (Text-fig. 8) plus interclavicle. FM PR 1745 (Text-fig. 3): seven articulated vertebrae. FM PR 1766: left scapulocoracoid with partial cleithrum. FM PR 1809: large skull with lower jaws, occiput preserved in three dimensions (Text-fig. 2); snout compressed anteroposteriorly and twisted around 90° to left. FM PR 1813: skull and vertebral column, with scattered girdle elements and limbs. FM PR 1814: partial skull with left lower jaw. FM PR 1816: articulated vertebral column, from cervicals approximately through first fifteen caudals, plus limb and girdle elements (pectoral girdle in Text-fig. 6); numerous ribs, some in articulation; associated with braincase and posterior half of skull table. FM PR 1880: left scapulocoracoid with cleithrum, left ilium and ischium, 15 articulated vertebrae and two disarticulated ribs. FM PR 1887: nearly complete articulated vertebral column plus associated pelvis and femur. FM PR 1889: complete rib from mid-presacral region (Text-fig. 5), associated with fragmentary postcranial elements on limestone block. FM PR 1957 (Text-fig. 7A): interclavicle. FM PR 1958 (Text-fig. 9): left femur. SUI 52010: five intercentra, five pleurocentra, including some small complete intercentra.

*Horizon and Locality.* Fills within two adjacent collapse structures formed in the Waugh and Verdi Members of the Iowa 'St Louis' Limestone. Mississippian, Lower Chesterian; correlative with the Lower Carboniferous,



Viséan V3b, Asbian, of Europe. Quarry on land owned by Mr Jasper Hiemstra, SW1/4, SW1/4, section 15, T75N, R13W, Keokuk County, Iowa, USA.

*Diagnosis.* Primitive tetrapod characterized by the following autapomorphies: ornament on cranial dermal bones extremely light, with frontal, parietal, and postparietal unornamented even on largest specimens; parietal foramen large relative to skull size; prefrontal forming thick, raised ridge at anterodorsal margin of orbit, with massive ventral projection on deep surface enclosing a large sinus(?); cleithrum terminating posterodorsally as a robust backwardly-directed process above a deep notch.

*Derivation of name.* After Delta, Iowa, USA, the town closest to the quarry where the type and all other known *Whatcheeria* specimens were collected.

## DESCRIPTION

### *Skull and Lower Jaw*

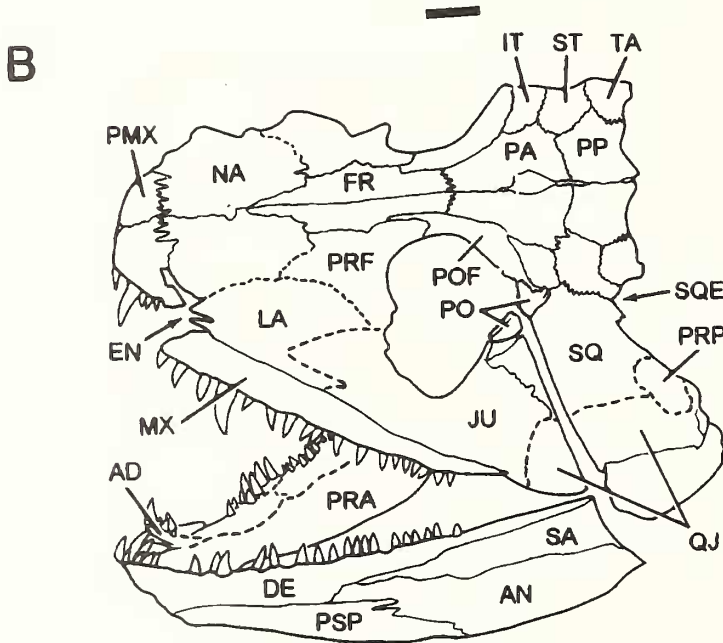
*General features.* Preliminary reconstructions suggest that the skull is high, with a significant degree of lateral compression and nearly vertical cheek. Most *Whatcheeria* skulls that retain the skull table and both cheeks, including the type, are crushed so that one cheek is folded under and the other is splayed out to the side as would be expected from a skull of this shape (Pl. 1; Text-fig. 1). The postoccipital portion of the cheek is very long, placing the jaw joint well behind the occiput. Postoccipital cheek length may be characterized as the horizontal (in the plane of the skull table) distance between the posterior extremities of the quadrate condyles and the posterior margin of the postparietals, divided by overall skull length expressed as horizontal distance from the quadrate condyles to the tip of the snout. On the type specimen, postoccipital cheek length is 21 per cent. of overall skull length. The snout is bluntly pointed rather than broadly rounded, as indicated both by skulls with this region intact and by the well-preserved symphysial region of the lower jaws in FM PR 1809.

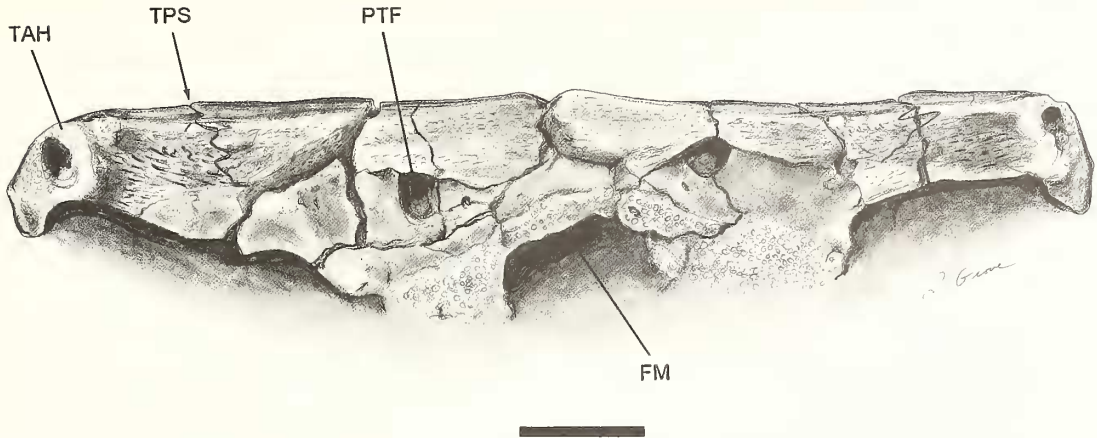
The centres of the large, quadrangular orbits lie at about 60 per cent. of the horizontal distance from the snout to the end of the skull table, as best seen in the holotype (Pl. 1) and FM PR 1634 (Text-fig. 1). Quadrangularity may be accentuated to some degree by crushing but is certainly real, as even isolated jugals and prefrontals always preserve the posteroventral and anterodorsal angles of the orbital margin, respectively. No scleral ossicles have been found. The external naris is far down on the side of the snout, just above the tooth row.

Cranial dermal ornament is very weakly developed. With the exception of the anterior one-half of the lower jaw, the external dermal bones are almost completely devoid of ornament. The course of the cranial lateral line system is indicated by canals completely encased in bone, or by open sulci which may be separated by regions of smooth bone that lack either sulci or canals. A linear array of circular foramina indicates the path of the canal where it is completely enclosed. This condition is best developed in the mandibular line along the anterior two-thirds of the lower jaw, and in the infraorbital line of the lacrimal and jugal. Elsewhere the course of the lateral line is primarily in segments of open sulci, interrupted by short segments of both enclosed canals and smooth bone (Text-fig. 1).

*Skull table.* The skull table comprises paired frontals, parietals and postparietals along the midline, bounded laterally by a temporal series of postfrontals, intertemporals, supratemporals and tabulars. This part of the skull is often found isolated and more or less intact, and is almost always present if any other skull roofing bones are preserved in articulation with one another. There is no tabular-parietal contact; the tabular and parietal are separated by the postparietal and supratemporal. As preserved, the skull table is planar. The posterior margin of the dorsal surface is roughly straight, as are its lateral margins posterior to the orbits. In dorsal view, the lateral and posterior margins are at right angles to one another. The lateral margins are formed by a pronounced ventral flexion which spans the intertemporal, supratemporal and tabular. Anterior to these elements, the skull table narrows sharply where it is incised by the dorsal margins of the orbits (Text-fig. 1).

The midline suture of the skull table is carried on a ridge from the posterior border of the postparietals to the anterior termination of the parietals, where it merges into the surface on either side of the midline. Posterior to the parietal foramen, the ridge broadens slightly. On either side of the midline ridge there is a broad, shallow depression on the postparietal and another on the parietal. The parietal foramen is rimmed by a raised ridge, which is slightly roughened in contrast with the smooth surrounding bone. The opening is exceptionally large,





TEXT-FIG. 2. *Whatcheeria deltae* gen. et sp. nov., FM PR 1809 (partial illustration), occipital region. Abbreviations: FM, foramen magnum; PTF, posttemporal fenestra; TAH, tabular horn; TPS, tabular-postparietal suture. Scale bar represents 10 mm.

and tear-drop shaped with its narrow end posterior. In these features, *Whatcheeria* is similar to *Proterogyrimus* as described by Holmes (1984), though the parietal foramen is larger in *Whatcheeria*. The parietal of the osteolepiform panderichthyid *Elpistostege* is also similar, although the parietal foramen is smaller than in either *Proterogyrimus* or *Whatcheeria* (Schultze and Arsenault 1985).

The 'tabular horn' has in recent decades been an important character in anthracosauroid systematics. In *Whatcheeria* the horn is short, and projects straight backward from the posterolateral corner of the tabular. It has previously been characterized (Bolt *et al.* 1988; Bolt 1990) as being of 'anthracosaur type,' as defined by Panchen (1985, p. 551). Now that more mature specimens are available, this characterization can be recognized as only partly correct. The horn is anthracosaur-like in that its dorsal surface is a continuation of the dorsal surface of the tabular. However, the bifurcation into 'superficial and (small) deep components' described by Bolt (1990, p. 346) reflects size (and perhaps individual variation as well). The largest specimens available, such as FM PR 1809, show that the terminus of the tabular horn is actually a large rimmed pit (Text-fig. 2). In some specimens, the lateral and medial portions of the pit wall are less well developed than the dorsal (especially) and ventral portions, giving rise to a misleading appearance of weak bifurcation. In addition to the rimmed pit that terminates the principal tabular horn, there is usually a smaller raised rugose area on the body of the tabular ventral to the tabular horn (Text-fig. 2). On the left side of FM PR 1809, an exceptionally large individual, a small rugose-surfaced protuberance arises from the dorsomedial side of the base of the tabular horn as well (Text-fig. 2).

*Cheek.* The cheek comprises postorbital, squamosal, jugal, quadratojugal and preopercular. It is particularly well preserved in the type and in FM PR 1813 and FM PR 1634. The jugal is excluded by the maxilla from the ventral margin of the cheek. There is a large squamosal embayment, bounded by the squamosal, supratemporal and tabular. The tabular forms the dorsal and anterodorsal margins of the embayment. The supratemporal

TEXT-FIG. 1. *Whatcheeria deltae* gen. et sp. nov., FM PR 1634 (partial illustration), skull and jaws as preserved. A, indicates surface texture, three-dimensional features and the morphology of the lateral line. Some postcranial elements present on the specimen not illustrated. B, outline drawing to show locations of sutures. Sutures visible on the specimen are solid lines, sutures reconstructed from other material are dashed lines. Abbreviations: AN, angular; AD, adsymphysial; DE, dentary; EN, external narial opening; FR, frontal; IT, intertemporal; JU, jugal; LA, lacrimal; MX, maxilla; NA, nasal; PA, parietal; POF, postfrontal; PO, postorbital; PMX, premaxilla; PP, postparietal; PRA, prearticular; PRF, prefrontal; PRP, preopercular; PSP, postsplenial; QJ, quadratojugal; SA, surangular; SQ, squamosal; SQE, squamosal embayment; ST, supratemporal; TA, tabular. Scale bar represents 10 mm.



forms only a small part of the anterior margin, as can be seen in, for example, the type and FM PR 1634. The cheek portion of the lateral line system preserves the primitive tetrapod pattern (Text-fig. 1).

The cheek-skull table junction of early tetrapods has traditionally been an area of particular functional morphological and phylogenetic interest, because it is often thought to be a kinetic joint inherited from osteolepiform crossopterygians (e.g. Carroll 1988). In *Whatcheeria* this suture is seen in several skulls and numerous separated bones. It shows no obvious characteristics of a mobile joint. On the contrary, the postorbital and squamosal form highly bevelled and interdigitated sutures with the postfrontal, intertemporal and supratemporal.

The preopercular spans the squamosal-quadratojugal suture on the posterior margin of the cheek. Although the sutures with these bones are often obscure, the preopercular can be distinguished from them by the orientation of the lineations on the surface of each. A well preserved preopercular occurs in FM PR 1636, where the suture between it and the squamosal is plainly visible. Another example is in FM PR 1644, which includes an associated quadratojugal and preopercular which have separated but are still in close proximity. The preopercular lateral line canal is represented by an open sulcus.

*Snout.* The snout comprises paired prefrontals, lacrimals, nasals, premaxillae and maxillae. Although a lateral rostral and/or anterior tectal might be expected in such a generally primitive tetrapod, neither has been recovered to date. However, adjacent surface features of the lacrimal and the nasal could indicate a suture with a tectal element.

The external naris is bordered by the maxilla, premaxilla, nasal and lacrimal. The maxilla and premaxilla form the smooth, finished edges of the posteroventral, ventral and anterior margins of the opening. The lacrimal forms only a small portion of the posterior narial margin. In the two specimens (FM PR 1634 and 1814) where the narial margin of the lacrimal is well preserved, it bears a very weakly incised depression. This depression continues for a short distance onto the adjacent portion of the nasal, the bone which forms the entire dorsal margin of the external naris. The nasal is flat to slightly upwardly convex above the opening, and its free margin is fimbriate, with a suture-like morphology. There is never a separate bone associated with this fimbriate area, despite the presence in the Delta collection of at least six prepared specimens that preserve the nasal portion of the external narial margin. It may nonetheless mark a suture, which would presumably be for an anterior tectal that might extend onto the lacrimal; this would be a primitive feature for tetrapods. On the other hand, the fimbriate area of the nasal might be a derived character, which would then be shared with *Archeria* (Holmes 1989) and *Pholiderpeton* (described as *Eogyrinus attheyi* by Panchen (1972)). The maxilla and premaxilla meet in a butt joint below the narial opening, with no sign of bevelling or interdigitation. Rather, the facing surfaces have the appearance of finished periosteal bone.

The prefrontal bears a prominent broad ridge at the anterodorsal corner of the orbit. This ridge is reminiscent of the 'eyebrow' of panderichthyid osteolepiform crossopterygians, in which it is developed on the postfrontal rather than the prefrontal (Schultze and Arsenault 1985; Vorobyeva and Schultze 1991). The undersurface of the prefrontal 'eyebrow' is a massive bony buttress containing spaces (sinuses?) from which small canals appear to open to the orbit via one or more foramina. This deep structure is hidden in almost all available *Whatcheeria* specimens, but is displayed in FM PR 1814. Crushing, combined with the presence of this resistant structure on the underside of the prefrontal, may enhance the prominence of the 'eyebrows' in *Whatcheeria*; it would be interesting to know whether a similar situation prevails in panderichthyids.

The premaxilla bears approximately five teeth + tooth spaces. One or two of these are large alternately replacing fangs, which are separated from the premaxilla-maxilla suture by one or two teeth or tooth spaces. The maxilla bears approximately 33 teeth + tooth spaces. A large fang or fang pair occurs anteriorly, at about positions 6–7 from the suture with the premaxilla. Except for the fangs, premaxillary and maxillary teeth are of similar sizes, decreasing gradually toward the posterior end of the maxillary tooth row. Both premaxillary and maxillary teeth and fangs are circular in cross-section near the base, with the usual labyrinthine appearance; the bases are externally striated. Both teeth and fangs are bluntly pointed and slightly recurved, with the curvature directed both medially and posteriorly.

*Occiput.* The following observations are based mainly on FM PR 1809 (Text-fig. 2), which preserves a relatively complete and undistorted occiput, and on FM PR 1652. The postparietals lack occipital lappets and appear not to be in contact with the exoccipitals, although we have not yet been able to identify either separated exoccipitals, or suture-bounded examples *in situ*. Both FM PR 1652 and FM PR 1809 appear to show the otic capsules in continuity above the foramen magnum. If this observation is correct, the exoccipitals would be physically precluded from contact with the postparietals. Well preserved, small posttemporal fenestrae are present on both sides in FM PR 1809; they appear to have been obliterated by crushing in FM PR 1652. Their

presence thus could be established only from the preservation of the opisthotics in a single specimen, as the several isolated skull tables available to us show no markings on the underside that indicate the existence of posttemporal fenestrae.

*Palate.* The palate is still poorly known; full description will require further preparation. The usual dermal bones are present, namely paired vomers, palatines, ectopterygoids, and pterygoids, plus a median parasphenoid with long cultriform process. The palate is bordered laterally by the premaxilla, maxilla and quadratojugal; the jugal is excluded by the maxilla from contact with any of the palatal bones. The pterygoids meet in the midline, excluding the other paired bones from the small interpterygoid vacuities. The elongate internal naris is bordered by the premaxilla, maxilla, vomer, and palatine.

The vomer, palatine, and ectopterygoid bear a single, nearly continuous row of about 20 teeth, approximately the same size as those of the marginal dentition. This row extends from the anterior end of the internal naris (which it passes on the medial side) to the posterior tip of the ectopterygoid. Only in the region of the vomer-palatine suture is there a slight diastema. Each of these bones also bears an alternately replacing fang pair in line with the other teeth, but no denticles. The palatal surface of the pterygoid is covered by a shagreen of denticles.

*Braincase.* The ossified portion of the braincase in *Whatcheeria* apparently comprises the otic capsules, exoccipitals, basioccipital, and basisphenoid, the latter tightly sutured to the parasphenoid. To date, we have identified eight more or less well-exposed braincases, some isolated and some preserved in association with skulls. Additional examples are demonstrably present in partial skulls, but are almost entirely covered by other bones and thus are not at present available for study.

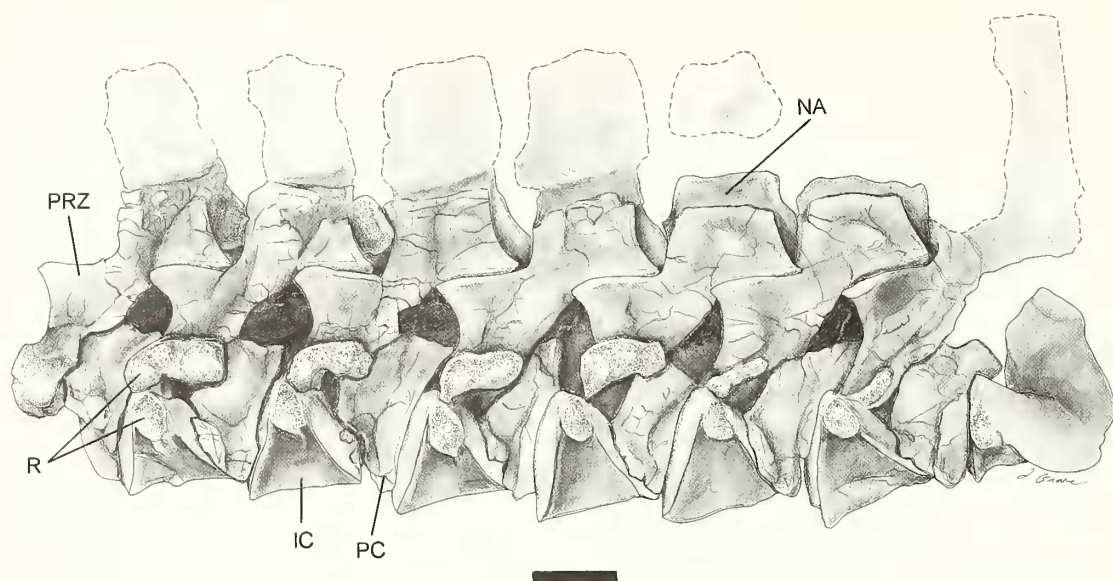
In ventral view, the posterior end of the parasphenoid is a posteriorly open 'U', with its base only a little posterior to the bases of the basiptyergoid processes. The braincases available to us that preserve the basisphenoid-parasphenoid unit in articulation with the basioccipital, suggest that the arms of the 'U' articulated at least as much with the lateral as with the ventral surface of the basioccipital. It appears that the basioccipital contact with the basisphenoid+parasphenoid complex was mostly a butt joint medially, with little overlap except via the arms of the 'U'. The cultriform process probably reached the pterygoids anteriorly. The basiptyergoid processes are very short, and in ventral view are covered by the parasphenoid up to the point where the articular surface begins. The articular surface is unfinished and bifaceted, with dorsal and ventral surfaces each of which is oriented as much laterally as anteriorly.

In FM PR 1651, both stapes are preserved in articulation with the braincase, which is seen in ventral view associated with the underside of the skull table. A single stapes is similarly preserved in FM PR 1816. All three stapes identified to date are badly crushed. The *Whatcheeria* stapes has a stapedia canal, and the ossified shaft as preserved appears flattened but not especially plate-like. However, the true extent of the stapedia shaft is unknown; the ventral margin in the available examples appears to be damaged or unfinished.

*Lower jaw.* The lower jaw has the overall shape common to that of many other early tetrapods, without the deep angle present in many anthracosauroids. There is no retroarticular process or 'coronoid process'. The jaw is composed of 12 bones: dentary, four infradentary bones (splenial, postsplenial, angular and surangular), adsymphyial, Meckelian bone, three coronoids, prearticular, and articular. Most of the sutures between these bones can be worked out from the numerous mandibles available.

On the external surface, the dentary extends from the symphysis through about two-thirds of the length of the adductor fossa. The infradentary bones are broadly exposed on the lateral surface (Text-fig. 1). Bones definitely participating in the symphysis include a Meckelian ossification, adsymphyial, and dentary; the sutures surrounding these bones are very clear. The splenial and/or prearticular may contribute as well, but in the specimens prepared to date the borders of the prearticular and splenial are ambiguous at the anterior end of the jaw. The adsymphyial rests in the symphyial curve of the dentary; it articulates posteriorly with coronoid I, and laterally with coronoid I, the dentary, and the Meckelian ossification. On the lingual surface the adsymphyial articulates with the prearticular(?) and Meckelian, and contributes to the symphysis. It bears a row of five to six small teeth along its lateral edge and a pair of marginal-sized teeth lingually.

The limits of the prearticular are clear where it articulates with the articular, coronoids and posterior three infradentary bones. The few large Meckelian fenestrae seen in some embolomeres are absent in *Whatcheeria*. Instead, the prearticular takes part in the formation of seven foramina along its articulation with the infradentary bones. The anteriormost foramen spans the splenial-postsplenial suture; the next four involve the postsplenial, and the last two may involve the postsplenial or angular. The two largest are in the postsplenial series. The suture between the prearticular and the infradentary bones is straight and not interdigitated. This



TEXT-FIG. 3. *Whatcheeria deltae* gen. et sp. nov., FM PR 1745, seven articulated presacral vertebrae as preserved. Abbreviations: IC, intercentrum; NA, neural arch; PC, pleurocentrum; PRZ, prezygopophysis; R, rib articulations. Scale bar represents 10 mm.

contact closely resembles those figured by Jarvik (1980) in *Ichthyostega*, and by Ahlberg *et al.* (1994) in *Ventastega*.

The three coronoids are lenticular in shape. Intercoronoid sutures are oriented longitudinally, running subparallel to the long axis of the jaw rather than transverse to it as is generally the case in osteolepiform fishes. Coronoids one and two bear two sizes of teeth. Each has a single longitudinal row of marginal-sized teeth along its lateral margin. These teeth are tallest in the centre of the row, and separated from the teeth on adjacent coronoid(s) by diastemas centred on the intercoronoid sutures. In addition, each bears a patch of denticles medial to the tooth row. Coronoid three bears marginal-sized teeth in a manner similar to the first two. A large patch of denticles occurs medial to these teeth, however, it is not possible at this time to determine whether they are borne on coronoid three or the prearticular.

Each dentary bears some 30–40 marginal teeth, the size and morphology of which are similar to those of the teeth of the upper marginal dentition. Height of the dentary teeth decreases slightly toward the adductor fossa, but is otherwise uniform. Each dentary has a pair of parasymphysial fangs just lingual to the marginal dentition in the symphyseal curve. The prearticular appears to lack denticles entirely, with the possible exception discussed above.

### *Axial skeleton*

The *Whatcheeria* material includes numerous examples of ribs and vertebrae, including long series of articulated vertebrae representing both presacral and caudal regions. The atlas and axis appear to be present in at least two specimens (FM PR 1634 and 1701), but accurate interpretation of their morphology will require further preparation. Because most of the articulated vertebral material is still unprepared, the composite description below depends primarily on two specimens: FM PR 1700 (Plate 1), and FM PR 1816 (not illustrated). Both have a single long series of articulated and mostly well preserved vertebrae, but neither includes the atlas.

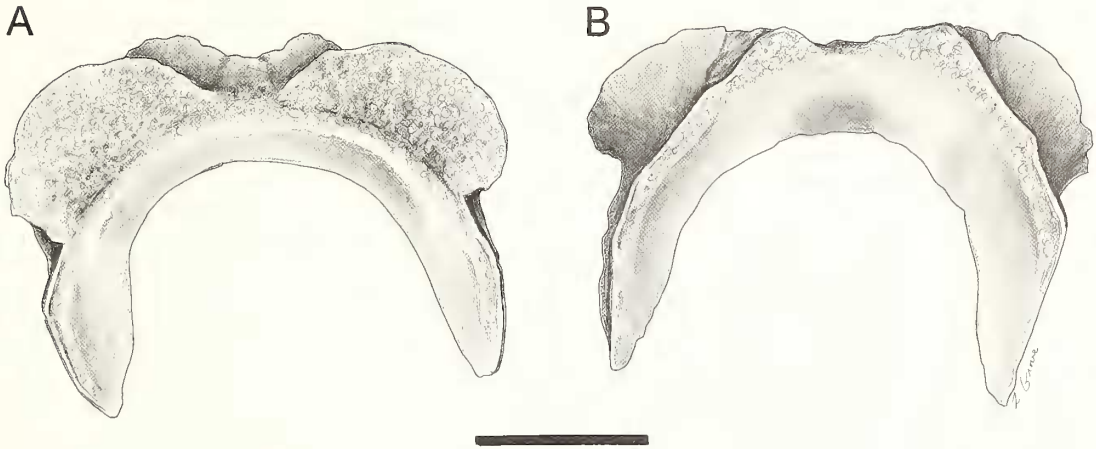
In FM PR 1816, all vertebrae are preserved in lateral view. The single sacral vertebra and rib are unequivocally identifiable. There are 14 caudals, which is less than the full number as shown by other, less completely prepared specimens. Twenty-four presacrals are clearly identifiable, and one vertebra anterior to these is represented by a crushed, featureless but vertebra-sized bony mass associated with a rib. Anterior to that vertebra, a further two are covered by an unidentified bone, but their presence is indicated by partial ribs



which continue the rib series visible on the other anterior vertebrae. The maximum presacral vertebral count for this specimen is thus 27. This is certainly less than the full count, but probably not by much (perhaps three or four at most), as suggested by the size and shape of the anterior ribs. We thus estimate that *Whatcheeria* has about 30 presacrals.

FM PR 1700, the holotype, preserves an articulated series of 22 presacrals, which starts 25 mm behind the skull table and does not include either the atlas or the sacral. The posterior 13 vertebrae in this series are preserved in lateral view, but the anterior portion of the column is twisted so that the first nine vertebrae are preserved in dorsal view, showing little more than their (badly crushed) neural arches.

Typical *Whatcheeria* vertebrae are composed of a crescentic, ventrally thickened intercentrum; paired(?) pleurocentra which extend far ventrally and are often fused dorsally; and a neural arch whose right and left halves are completely fused (Text-figs 3-4). Both pre- and postzygapophyses of presacral neural arches are



TEXT-FIG. 4. *Whatcheeria deltae* gen. et sp. nov., FM PR 1712, pleurocentrum. A, anterior, and B, posterior view. The large articular surfaces for the preceding neural arch are visible in anterior view, the smaller surfaces for the succeeding neural arch in posterior view. Scale bar represents 10 mm.

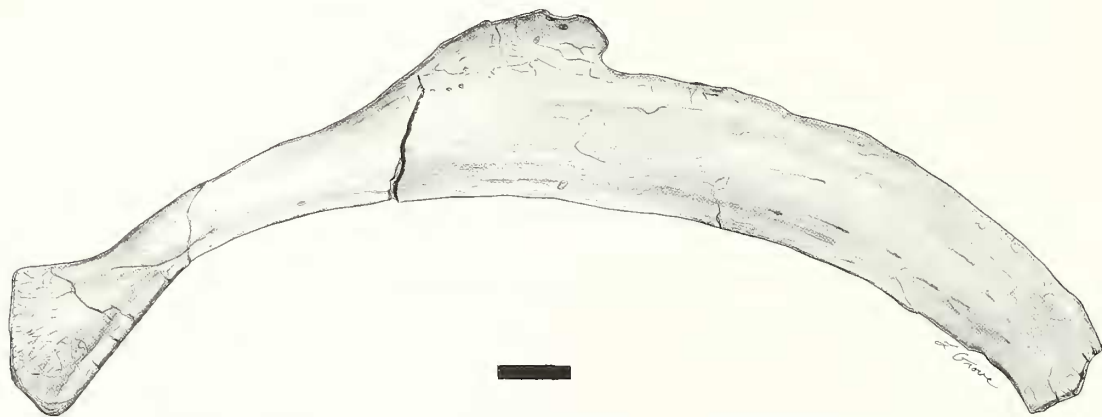
'well developed' in the sense that their cranial-caudal dimension is equal to or larger than that of the neural arch at the same level. Zygapophyses of the caudal vertebrae preserved in FM PR 1816 are also well developed, but diminish significantly in size posteriorly. A supraneural canal is preserved in the neural arch. The neural spines on the caudal vertebrae of FM PR 1816 are slightly (10 mm) taller than those on the presacrals.

The intercentra are not unusual. The dorsally fused pleurocentra, on the other hand, are remarkable. Most of the fused pleurocentra we have seen are separated specimens. Each example bears a large pair of anteriorly facing articular facets for the preceding neural arch, and a small pair for the succeeding one (Text-fig. 4). Fused pleurocentra have been found in a variety of sizes, including some that are quite small. For example, the pleurocentrum in Text-fig. 4 is about 30 mm in greatest diameter, compared with about 15 mm in one of several examples catalogued as SUI 52010. Given that we have a number of articulated *Whatcheeria* vertebral series, it might seem that the frequency and regional variations of fused pleurocentra could be easily determined. However, it is difficult to examine pleurocentra *in situ* in articulated specimens, as this would generally require destructive preparation. We have at present only one *Whatcheeria* specimen that demonstrates some fused pleurocentra as part of an associated vertebral series. In FM PR 1887, four or possibly five dorsally-fused pleurocentra are visible in a disrupted and somewhat scattered region of an otherwise articulated column, just anterior to the sacral vertebra. Three of these are still in close association with the intercentrum, although apparently not fused to it, thus making a bipartite centrum. In articulation, these two central elements form an amphicoelous centrum with a very restricted notochordal opening that is about 20 per cent. of the total centrum diameter. Some *Whatcheeria* vertebrae may be monospondylous: we have recovered an isolated

example tentatively identified as *Whatcheeria*, in which the pleurocentrum is fused to the intercentrum behind it, without trace of suture (FM PR 1886). This specimen is broken in such a way as to make it uncertain whether the pleurocentra were fused across the dorsal midline as well as to the intercentrum. Pleurocentra which fuse dorsally but not ventrally, or are components of a monospondylous centrum as described above, have been described as occurring occasionally in a few temnospondyls (Shishkin 1989).

Presacral rib morphology is one of the most striking features of *Whatcheeria*. FM PR 1700 retains most of the presacral ribs in association with the (preserved portion) of the column (Pl. 1). Most of the presacral ribs are missing in FM PR 1816. It does retain a few in association with their vertebrae, however, at the anterior end of the articulated series and immediately anterior to the sacral vertebra. In addition to the sacral, the first four caudal ribs are present in FM PR 1816. Corresponding vertebrae in FM PR 1816 and FM PR 1700 can be identified based on rib morphology. In FM PR 1816, the most-anterior vertebra whose rib bears a small uncinat process is number 23 anterior to the sacral (sacral vertebra = no. 0). A similar rib in FM PR 1700 is also very near the anterior end of the preserved portion of the column. If this correlation is accepted provisionally, it follows that FM PR 1700 preserves vertebrae from number 6 to number 27 anterior to the sacral, while FM PR 1816 preserves vertebrae number 1 to number 27 anterior to the sacral, plus the sacral itself and the first fourteen caudals.

Changes in *Whatcheeria* rib size and shape, from anterior to posterior, are approximately as follows. We are uncertain whether the atlas bears ribs, but all other presacral vertebrae probably do. Anterior ribs are short, thin, and nearly straight, with a shaft some 2–3 mm in diameter near the head, and not markedly flattened in cross-section. Beginning at vertebra no. 23 anterior to the sacral, the shaft flattens markedly, ribs become longer and strongly curved, and uncinat processes appear proximally, about 20 mm distal to the head. They enlarge rapidly and extend progressively further distally, becoming flanges rather than processes. At the point of greatest development of these flanges, around no. 20 anterior to the sacral, *Whatcheeria* ribs resemble those of *Ichthyostega* (Jarvik 1980), although they are not quite as large (Text-fig. 5). Posteriorly from their point



TEXT-FIG. 5. *Whatcheeria deltae* gen. et sp. nov., FM PR 1889, a rib from mid-trunk as preserved. Scale bar represents 10 mm.

of maximum development, the flanges diminish rapidly. By about no. 11 anterior to the sacral the ribs lack flanges even as 'uncinat processes' and are diminishing rapidly in length and shaft diameter. Ribs immediately anterior to the sacral vertebra are very small, almost rudimentary.

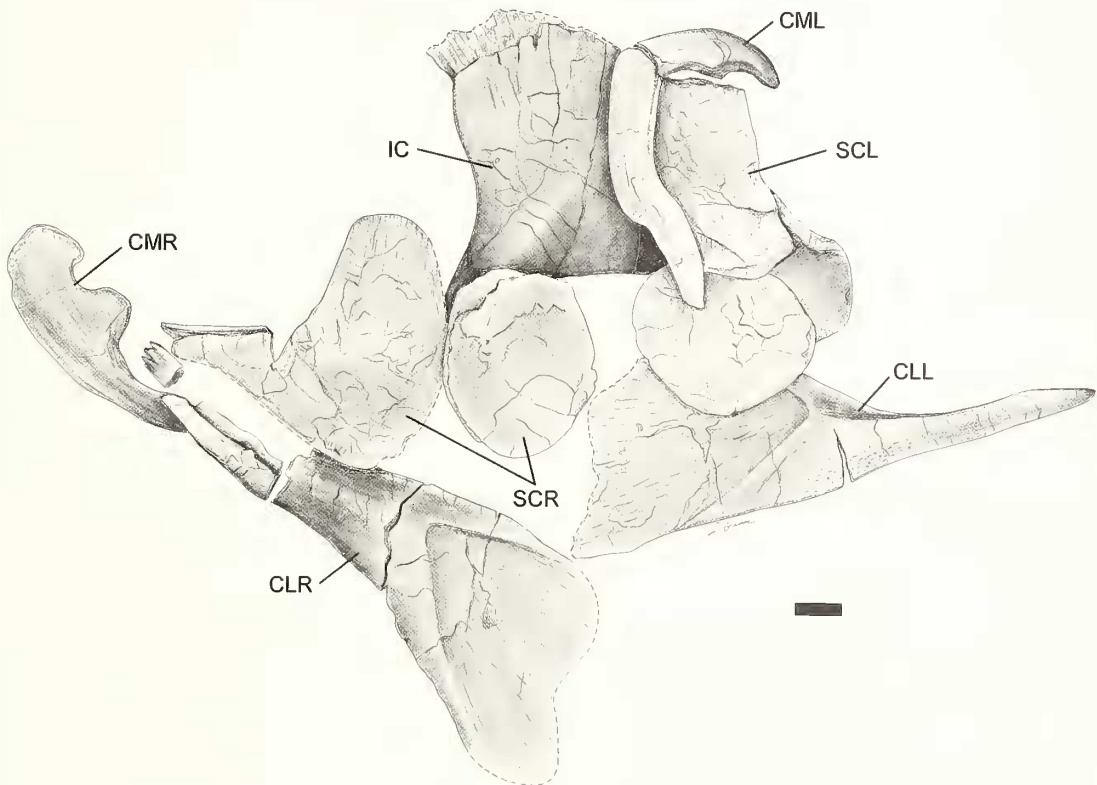
The sacral rib is short and massive, and borne on a greatly enlarged diapophysis. The first caudal vertebra bears a robust, slightly curved rib, whose shaft is semicircular in cross-section with a diameter of about 5 mm. Ribs on caudals 2–4 are slightly larger and longer, and progressively curved more and more strongly posteriorly. The distal half of the fourth caudal rib is angled at about 80° to the proximal half; overall length of this rib as preserved is about 80 mm. Although no ribs are preserved posterior to this point, they might have been present on a few additional caudals; caudal no. 8 is apparently the last vertebra with even a rudimentary diapophysis. The first haemal arch preserved is in association with caudal no. 7, although detached from its intercentrum. Haemal arches probably began anterior to this, as the intercentrum of caudal no. 6 clearly has

the appropriate facet on its posteroventral corner. In FM PR 1816, haemal arches are present on caudals 8–14, which is the last vertebra preserved.

*Appendicular skeleton*

*General.* Relative to overall body size, the limbs of *Whatcheeria* are as large as those of embolomeres and most other early anthracosaurs. Each has well developed tetrapod-type digits. Combined measurements from FM PR 1700, the holotype, and FM PR 1816 indicate that the limbs are of equal length as measured from the proximal end of the propodial to the distal ends of the epipodials. All articulated and most isolated specimens of the pro- and epipodial bones are more or less crushed, through some beautifully preserved three dimensional examples have been recovered as isolated specimens from limestone matrix. No mesopodial elements have yet been recognized, and they may have been unossified. There is no evidence for more than five digits, but the few associated, articulated hands and feet so far available are probably incomplete. All digits are composed of short, flat phalanges, which gives the manus and pes a paddle-like appearance.

*Forelimb.* The pectoral girdle is composed of a midline interclavicle flanked on either side by a scapulocoracoid, clavicle, and cleithrum (Text-figs 6, 7A). The external surfaces of interclavicle, clavicle, and cleithrum are



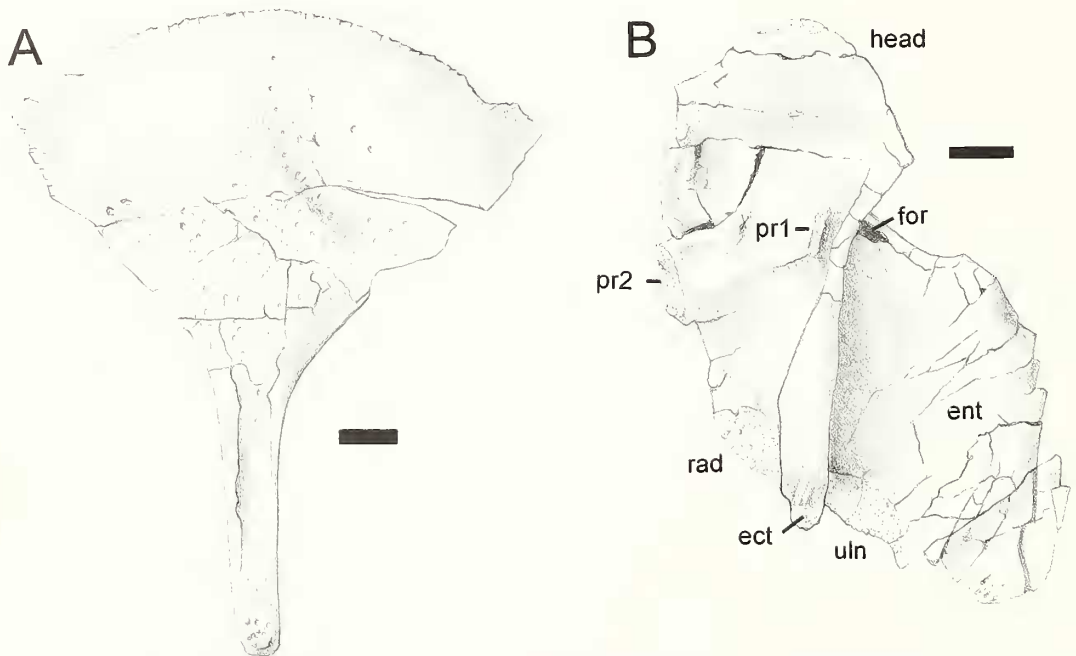
TEXT-FIG. 6. *Whatcheeria deltae* gen. et sp. nov., FM PR 1816, pectoral girdle as preserved. Abbreviations: CLR, CLL, right and left clavicles respectively; CMR, CML, right and left cleithra, respectively; IC, interclavicle; SCR, SCL, right and left scapulocoracoids, respectively. The clavicles are seen in internal view, with anterior roughly towards the bottom of the page. The large, triangular articular depression for the interclavicle is evident on both. The right cleithrum is seen in internal view, the left mostly in anterior view. The interclavicle is exposed in dorsal view. The bone has been rotated by about 90° counterclockwise relative to the other elements, so that its anterior end is roughly towards the upper right of the drawing. The parasternal process lies beneath the other elements present and is oriented towards the lower left of the figure. The right scapulocoracoid is exposed in internal view, the left in external view. Each scapulocoracoid is composed of two ossifications. Scale bar represents 10 mm.



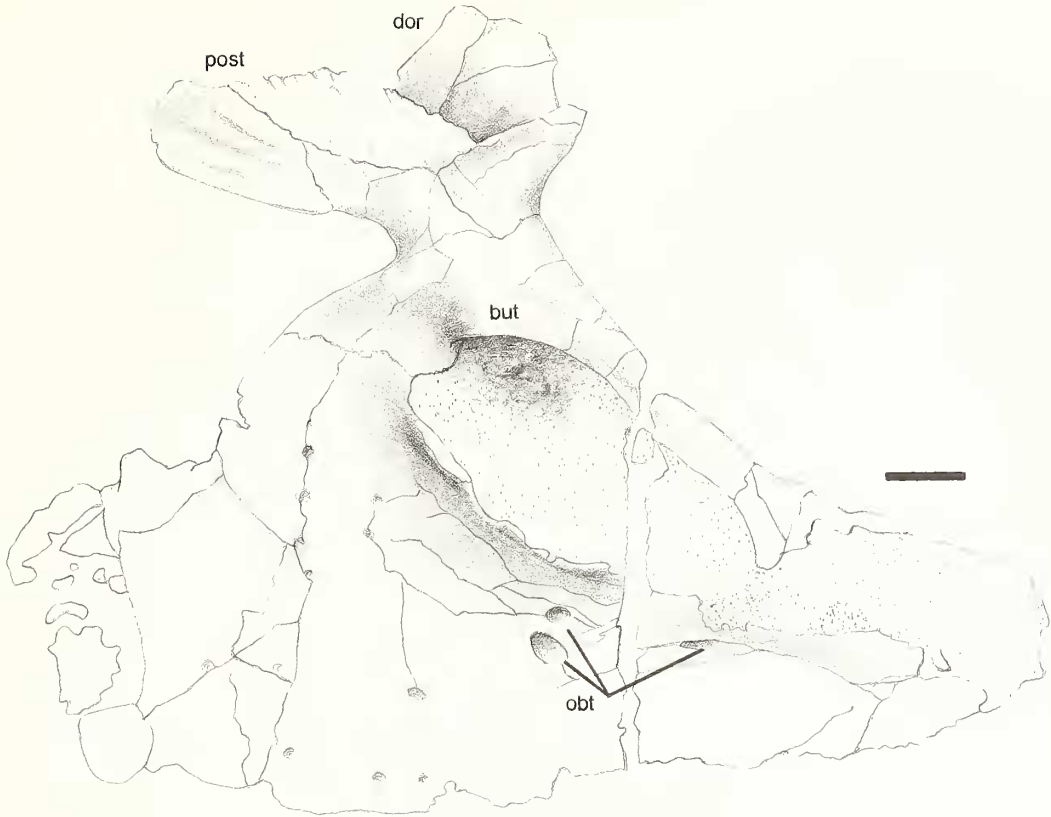
unornamented. The roughly diamond-shaped body of the interclavicle is wider than long, and the long, slender parasternal process is slightly longer than the body. The anterior facets on the external surface of the interclavicle indicate that the clavicles met at the midline at least over the anterior portion of that bone. The cleithrum completely caps the dorsal border of the scapulocoracoid. As an apparently autapomorphic feature of *Whatcheeria*, the cleithrum has a deeply incised, rounded notch in its posterior border. The notch accentuates the blunt-tipped, posteriorly directed process which terminates the cleithrum's posterodorsal extremity. There is evidence for a postbranchial lamina on the cleithrum: FM PR 1766 is a three-dimensional partial scapulocoracoid, which preserves the ventral portion of the cleithral shaft in articulation with the anterior edge of the scapulocoracoid. The anterior edge of the shaft forms a distinct, medially-inturned flange that appears comparable to that described in *Acanthostega* by Coates and Clack (1991). The postbranchial lamina does not appear to extend onto the clavicle.

The scapulocoracoid apparently ossified from two centres, a scapular and a coracoidal. In FM PR 1816 (Text-fig. 6), the scapula and coracoid of each side are preserved as separate but closely associated ossifications. FM PR 1704 is an isolated left scapulocoracoid with the distinctive cleithrum in its normal position. Here the scapulacoracoid is a single piece, with no trace of suture; a deep and apparently natural notch on its anterior border at the dorsoventral level of the glenoid may mark the boundary between two ossification centres. A left scapulocoracoid with similar notch occurs in FM PR 1635, in association with a *Whatcheeria* skull and partial postcranium. Glenoid shape is comparable to that in many other primitive tetrapods: the glenoid is anteroposteriorly elongate and helical. There is a supraglenoid foramen and a supracoracoid foramen, both opening into the subscapular fossa.

Description of the humerus is complicated by the fact that all of the humeri associated with unequivocal *Whatcheeria* remains are crushed, and most are nearly featureless, with poorly ossified proximal and distal ends. The left humerus associated with *Whatcheeria* skeleton FM PR 1635 and prepared in extensor view is a partial exception, in that the caput, capitellum and trochlea, as well as the ectepicondyle and entepicondyle plus some other processes, are all fairly well developed and relatively well preserved. This specimen (Text-fig. 7B)



TEXT-FIG. 7. *Whatcheeria deltae* gen. et sp. nov., pectoral limb elements. A, FM PR 1957, interclavicle in external view. Anterior is to the top of the page. B, FM PR 1635, extensor surface of left humerus. Proximal is to the top of the page. Abbreviations: ect, ectepicondyle; ent, entepicondyle; for, entepicondylar foramen; pr1, process usually identified as a 'latissimus dorsi process;' pr2, process usually identified as a 'deltoid process;' rad, radial articulation; uln, ulnar articulation. Scale bars represent 10 mm.



TEXT-FIG. 8. *Whatcheeria deltae* gen. et sp. nov., FM PR 1740, right half of pelvic girdle. Dorsal is to the top of the page, anterior to the right. Abbreviations: but, acetabular buttress; dor, dorsal iliac process; obt, obturator foramina; post, postiliac process. Scale bar represents 10 mm.

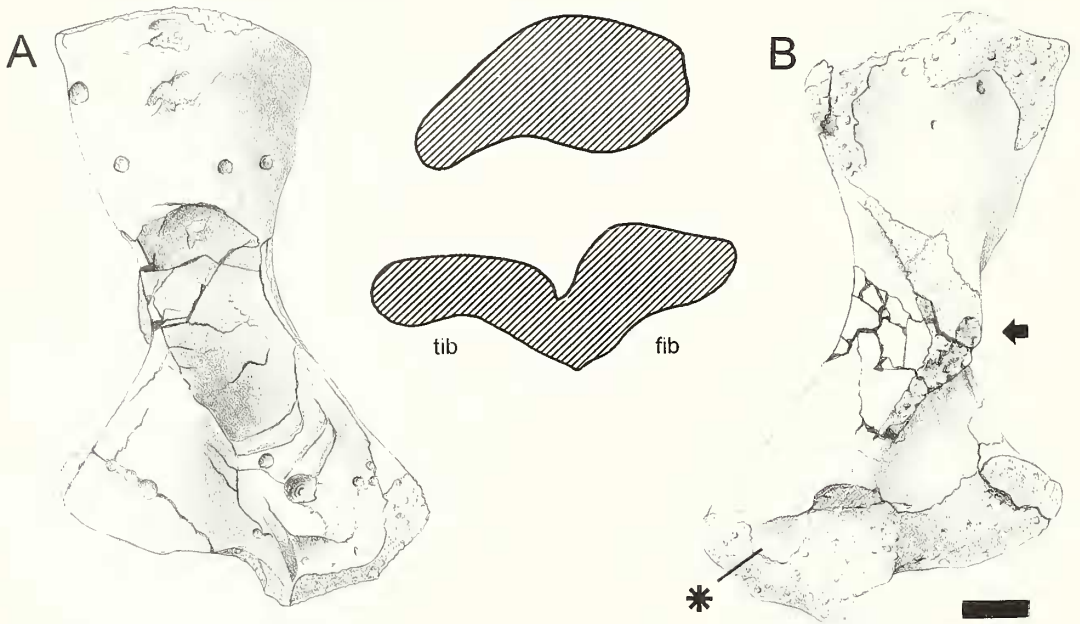
represents the midpoint, in size and ossification, between other definite *Whatcheeria* humeri and some larger and better preserved but unassociated humeri of similar morphology. Although it is thus not established beyond doubt, especially as two other taxa of similar body size are known to occur at the Delta site, we believe that the members of this series all pertain to *Whatcheeria* and base the following description on that belief.

The humerus is the standard early tetrapod L-shaped bone, the shape resulting from the presence of a very large, squared-off entepicondyle. In *Whatcheeria*, both the anteroposterior and proximal-distal dimensions of the entepicondyle are approximately equal to humeral length along the shaft, the latter being, in fact, hardly discernible as such. The ectepicondyle is an exceptionally prominent projection at the distal end of a ridge that begins near the humeral head. On the anterior edge of the shaft there is a distinct 'deltoid' process (pr2, Text-fig. 7B), and a distinct 'latissimus dorsi' process (pr1, Text-fig. 7B) arises from the extensor surface at about mid-shaft; in large specimens, this is developed as a prominent spinous process. The flexor surface bears a very large pectoralis process near its anterior edge (not illustrated). No 'supinator' process can be distinguished. There is a large entepicondylar foramen, but no ectepicondylar foramen. The capitellar and trochlear articular surfaces, for articulation of the radius and ulna respectively, are visible in both flexor and extensor view. The radius and ulna are robust bones, the latter with a well developed olecranon process.

*Hindlimb.* The pelvic girdle has well developed dorsal iliac and postiliac processes (Text-fig. 8). The dorsal iliac process undoubtedly articulates with the markedly robust, short, single sacral rib. The postiliac process is everted from the lateral face of the dorsal process, producing a smooth-surfaced, U-shaped channel between the two processes. Much of the lateral face of the postiliac process is heavily ridged. The ridges run

anteroventrally from the dorsal edge of the process. The acetabulum is anteroposteriorly elongate, strongly concave, and floored by unfinished bone. Posterodorsally, a prominent buttress overhangs the acetabulum. Just posterior to the buttress is a small tongue of finished bone that projects into the acetabulum. Anterior to the acetabulum is a large anteroposteriorly elongate area of unfinished bone separated from the acetabulum itself partly by dorsal and ventral projections of finished bone and partly by an elevated ridge of unfinished bone. The ventral margin of the acetabulum forms a prominent ridge and just ventral to that ridge are three obturator foramina. None of the pelvis prepared so far preserves evidence of the number of ossifications contributing to the pelvic girdle. Neither within the acetabulum nor anywhere else on the girdle have we yet found any trace of a suture. On the other hand, one example of a *Whatcheeria* pelvic girdle (FM PR 1880) includes an apparently independent ilium in lateral view, accompanied by a free bony disc in the expected position of an ischium. Identification of this element is uncertain, as neither it nor the (indisputable) ilium bear any trace of an acetabulum, probably due to immaturity.

The femur is of comparable size to the humerus in specimens where both are preserved (FM PR 1700 and FM PR 1816). All *Whatcheeria* femora that have been prepared to date are more or less severely crushed, like that in the holotype, FM PR 1700 (Pl. 1). An isolated, relatively well preserved femur, FM PR 1958 (Text-fig. 9), compares in all respects with those associated or articulated with definite *Whatcheeria* specimens, and the



TEXT-FIG. 9. *Whatcheeria deltae* gen. et sp. nov., FM PR 1958, left femur. A, extensor surface. B, flexor surface. For each, proximal is towards the top of the page. Between the two drawings are plane projections of the proximal (upper) and distal (lower) regions of unfinished bone. For both, the extensor surface is uppermost. Arrow indicates the approximate highpoint of the adductor crest; asterisk indicates a small region of finished bone discussed in the text; fib, indicates the articular region of the fibula; tib, the same for the tibia. Scale bar represents 10 mm.

following description is based primarily on this example. The shaft is short and stout, and both the proximal and distal ends are expanded. The articulation for the fibula projects further distally than that for the tibia, and flares posteriorly such that the postaxial border of the femur is more deeply concave than the preaxial border. The extensor surface is relatively featureless but is marked by a deep furrow that separates the condyles distally. In FM PR 1958 the marrow cavity of the shaft has collapsed, leaving an elongate depression, and both the proximal and distal ends are marked by linearly arrayed, circular punctures interpreted as tooth marks resulting from scavaging or predation (see below). In flexor view, a prominent oblique ridge, *sensu* Jarvik 1980, begins just between the condyles distally and angles anteriorly and proximally to project beyond the preaxial



border at midshaft (arrow, Text-fig. 9). At this point, the ridge reaches its maximum elevation from the general surface of the shaft. From this apex, the ridge angles posteriorly and proximally and almost immediately bifurcates. The thicker, anterior ridge angles toward the anterior corner of the femoral head but rapidly decreases in height, ending about halfway to the head. The thinner, posterior ridge continues towards the posterior corner of the femoral head whilst gradually decreasing in height. A fossa occupies the area between the two ridges. No ridge or boss occurs in a position equivalent to that occupied by the internal trochanter commonly found in the femora of other Palaeozoic tetrapods. No tooth marks occur on the flexor surface, but a few small foramina are located near the proximal end. The fibular articulation is characterized by a small, strongly concave area of periosteal bone visible in flexor view (\*, Text-fig. 9). This feature occurs less prominently in some other primitive tetrapods; its condition in the Lower Carboniferous *Proterogyrinus* (Holmes 1984) is most similar to that in *Whatcheeria*. The tibia and fibula are similarly robust, with no remarkable distinguishing characteristics (Plate 1).

### *Scales*

A number of scattered, elongate bony scales have been recovered from the site, none in association with articulated *Whatcheeria* skeletal elements. On the other hand, numerous similar or identical scales are associated with the one articulated 'embolomere' skeleton recovered from the Delta site. A colosteid amphibian also occurs at Delta, though no definitely colosteid postcranial remains have so far been recognized. The colosteid *Greererpeton*, from the Lower Carboniferous of West Virginia, has bony scales, though of different morphology from the Delta scales (Romer 1972; Godfrey 1989). The implication, then, is that *Whatcheeria* does not have bony scales and the tetrapod-type scales so far recovered probably belong to the Delta 'embolomere.'

### *Evidence of predation or scavenging*

Both the pelvis and the femur illustrated here show features which we interpret as resulting from predation or scavenging (Text-figs 8–9). Both bones preserve linear arrays of circular depressions. The depressions are sometimes quite deep, and their size and spacing are comparable to those of the alternately replacing marginal dentition of both *Whatcheeria* and the undescribed colosteid at the site. On the extensor surface of the femur, there are two linear arrays at approximately right angles to the long axis: one proximally and one distally. The proximodistal spacing of these arrays is comparable to the head width of *Whatcheeria* obtained from a preliminary reconstruction. The distal array on the femur contains a larger and deeper puncture lying just off the axis of the smaller holes. This is consistent in size and position with having been made by a fang.

## DISCUSSION

For researchers concerned with the origin and early evolution of tetrapods, *Whatcheeria* is in many ways gratifyingly primitive and certainly ancient, representing a period from which few tetrapods have yet been described. It is thus no surprise that its relationships to other tetrapod groups, and the evolutionary history of some of its most striking characters, are far from obvious. Resolution of these uncertainties will require a level of detailed comparative study and cladistic analysis which are beyond the scope of this description. Consequently, the discussion below depends on cladistic studies of early tetrapods published by several other authors. We have relied upon papers with analysis founded on the now almost universal view, which we share, that osteolepiform fishes are the sister group of tetrapods. Within this broad consensus, various authors differ in the groups considered, characters analysed, and polarity assigned to the same characters, and consequently in the cladograms produced. We do not attempt to reconcile those differences here; instead, we confine our discussion for the most part to characters on which there seems to be substantial agreement. More problematic characters are noted and discussed as such.

*Whatcheeria* shows a number of characters that are primitive for tetrapods, but are absent in all but a few of even the earliest known tetrapods. Some of these characters are mentioned in the description above, but we have not attempted to enumerate all of *Whatcheeria*'s primitive characters. The following list provides an indication of its overall primitiveness, but is not intended to substitute for a thorough cladistic analysis.

1. The postoccipital portion of the cheek is long. In *Whatcheeria*, postoccipital cheek length is 21 per cent. of skull length. This is similar to the postoccipital cheek length of various osteolepiforms and primitive, early tetrapods, as calculated by us from reconstructions published by several authors. Thus among osteolepiform fish, postoccipital cheek length is about 19 per cent. of skull length in *Panderichthys rhombolepis* (based on Vorobyeva 1977) and 18 per cent. in *Eusthenopteron fordi* (based on Jarvik 1980). Among early tetrapods, postoccipital cheek length is 14 per cent. in *Ichthyostega* and 13 per cent. in *Acanthostega* (both based on Jarvik 1980); 28 per cent. in *Crassigyrinus* (based on Panchen 1985), which must hold the record for postoccipital cheek length among early tetrapods; 14 per cent., 12 per cent. and 11 per cent. respectively, in the loxommatids *Baphetes kirkbyi*, *Megalocephalus pachycephalus* and *Loxomma acutirhinus* (based on Beaumont 1977); 18 per cent. and 13 per cent. respectively, in the embolomeres *Proterogyrinus scheelei* (based on Holmes 1984) and *Pholiderpeton scitigerum* (based on Clack 1987); and 8 per cent. in the colosteid *Greererpeton burkendorfi* (based on Smithson 1982).

2. Presence of a preopercular. This is known to occur only in *Ichthyostega* (Jarvik 1980), *Acanthostega* (Jarvik 1980; Clack and Coates 1993); *Crassigyrinus* (Panchen 1985), and possibly in *Ventastega* (Ahlberg *et al.* 1994).

3. The lateral line is enclosed in bony canals in some places. Enclosed lateral line canals opening to the surface through spaced holes are universal in osteolepiform fish and occur to some degree in other primitive tetrapods, including the Devonian taxa *Acanthostega* (Jarvik 1980; Clack and Coates 1993), *Ichthyostega* (Jarvik 1980), *Ventastega* (Ahlberg *et al.* 1994) and *Elginerpeton* (Ahlberg 1995) and the Lower Carboniferous *Pholidogaster* (Panchen 1975), *Greererpeton* (Smithson 1982) and *Doragnathus* (Smithson 1980).

4. The dentary extends far posteriorly along the adductor fossa; its extent is comparable to that of dentaries in *Metaxygnathus* (Campbell and Bell 1977) and the loxommatids *Megalocephalus pachycephalus* and *Loxomma rankini* (Beaumont 1977). Only in *Ichthyostega*, which shows the most plesiomorphic state known for tetrapods, does the dentary extend further back (Jarvik 1980).

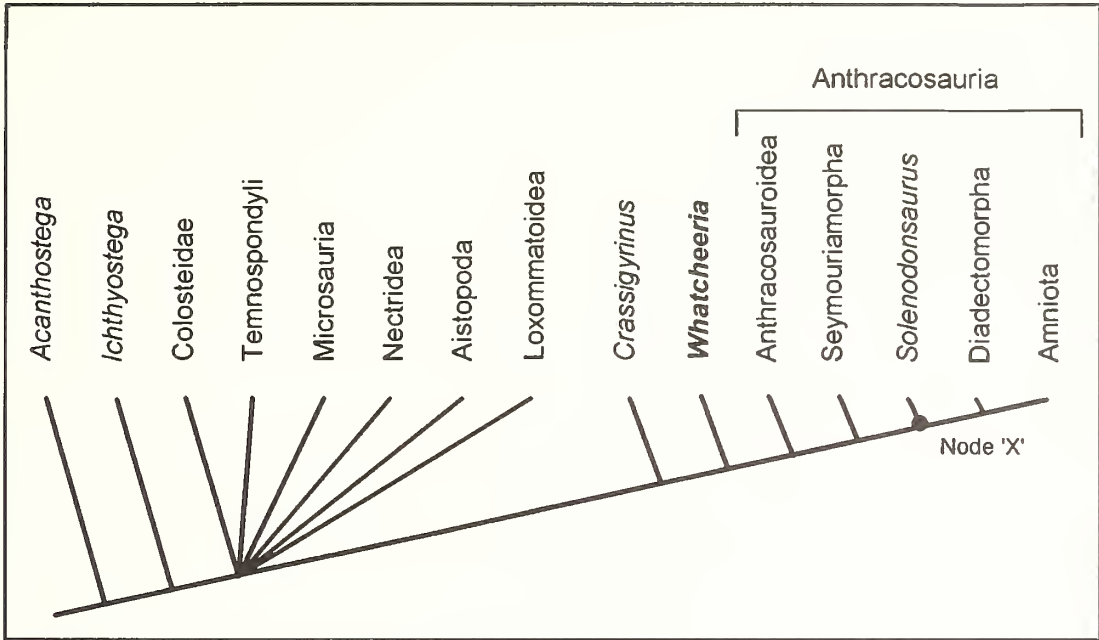
5. The prearticular extends far forward, coming very near to the symphysis and perhaps even participating in it. The prearticular in *Ventastega* also extends far forward (Ahlberg *et al.* 1994), although again it is uncertain whether it participates in the symphysis. It definitely does so in *Ichthyostega* (Jarvik 1980), and the panderichthyid fish *Panderichthys rhombolepis* (Vorobyeva and Schultze 1991).

6. An adsymphysial is present, which is also primitive in bearing teeth. An adsymphysial is very rare in tetrapods, though universal in osteolepiforms. It is present in *Ichthyostega*, where it was sketchily restored by Jarvik (1980), as well as in *Acanthostega* (J. A. Clack, pers. comm.). *Elginerpeton* from the Devonian of Scotland, is interpreted as having a toothed adsymphysial (Ahlberg 1995), as has *Ventastega* (Ahlberg *et al.* 1994), a tetrapod jaw from the Pennsylvanian of Nova Scotia (Godfrey and Holmes 1989) and the Lower Permian embolomere *Archeria* (Holmes 1989).

7. The small and numerous Meckelian foramina are similar to those in the osteolepiform *Panderichthys* (Vorobyeva 1962). Among tetrapods, *Ichthyostega* has been figured with five similar foramina (Jarvik 1980), *Ventastega* with at least three (Ahlberg *et al.* 1994; a minimum estimate, since the figured specimen is damaged), *Caerorhachis* with three (Holmes and Carroll 1977) and *Elginerpeton* with perhaps five, though in this case they are between the Meckelian ossification and the infradentary bones (Ahlberg 1995).

8. The tabular and parietal are not in contact, and in fact are widely separated. This configuration is widespread among early tetrapods, but the condition in *Whatcheeria* is noteworthy because apart from *Crassigyrinus*, it is unique in an animal that appears to have anthracosauroid affinities (see discussion below).

9. Each of the paired palatal bones bears a fang pair, which forms part of a row of about 20 marginal-sized teeth. This arrangement is similar to the condition in *Ichthyostega* and *Acanthostega*, though the distribution on individual bones is different (Jarvik 1980; Clack and Coates 1993; Clack 1994a). Most other Palaeozoic tetrapods have fewer marginal-sized teeth on the palate (or none).



TEXT-FIG. 10. Hypothesis of relationships of *Whatcheeria* to selected Palaeozoic tetrapod groups, as discussed in the text. Position of *Acanthostega* and *Ichthyostega* after Lebedev and Coates (1995). 'Node X' from Gauthier *et al.* (1988).

10. The femur has an oblique ridge on the flexor surface which reaches its maximum elevation at midshaft. This configuration has been described only in *Ichthyostega* among early tetrapods (Jarvik 1980). Indeed, the pattern of ridges and fossae on the flexor surface bears a striking resemblance to those illustrated for *Ichthyostega*. We hypothesize that this morphology is primitive for tetrapods.

11. The pelvis has a large area of unfinished bone anterior to the acetabulum. This feature has been illustrated for *Ichthyostega* by Jarvik (1980). The general shape of the acetabulum plus anterior unfinished area in *Whatcheeria* and *Ichthyostega* are remarkably similar with respect to proportions, orientation, and details of bony buttresses, including a small tongue of finished bone that projects into the acetabulum at its posterior end next to the large supracetabular buttress. The *Whatcheeria*-*Ichthyostega* configuration may be primitive for tetrapods.

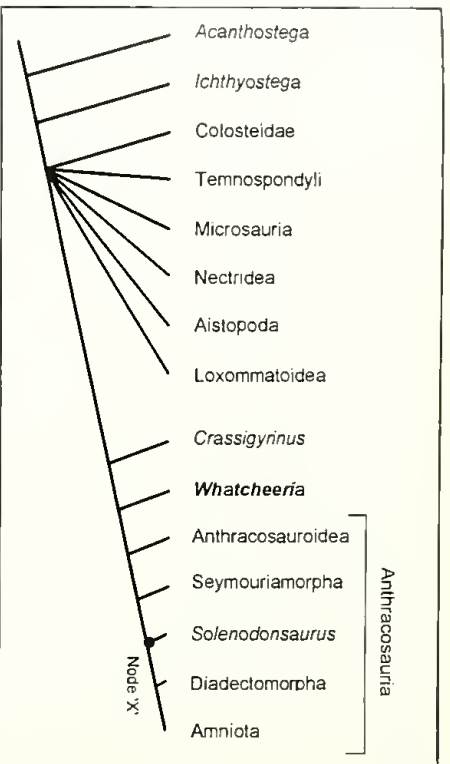
In the absence of a formal cladistic analysis, we will discuss *Whatcheeria*'s relationships first in terms of what it appears not to be, and then in terms of an informal analysis that suggests some groups to which it might be related. To begin, we note that we can identify no synapomorphies of *Whatcheeria* and the microsaurians, nectrideans, or aistopods. Similarly, no synapomorphy convincingly links *Whatcheeria* with temnospondyls. In particular, there is no postparietal-exoccipital contact, which (following Smithson 1985b) is characteristic of both temnospondyls and microsaurians. *Whatcheeria* also does not appear to form a natural group with either or both of two early tetrapod groups that may be called 'temnospondyl-like', namely the loxommatids and colosteids, nor does it share derived characters with any of the Devonian taxa so far described.

We can, however, identify plausible synapomorphies of *Whatcheeria* and Anthracosauria, two of which seem especially convincing:

1. The posttemporal fenestra is small (see discussion in Gauthier *et al.* 1988).
2. The upper surface of the tabular horn is a posterior extension of the upper surface of the tabular, i.e. both lie at the same dorsoventral level (see Panchen 1985).







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Seven additional characters seem to us to suggest a *Whatcheeria*–Anthracosauria relationship, but less convincingly so:

3. The temporal series in the skull table has an abrupt, strong ventral flexure that places the sutures for the cheek bones in a much more ventral plane than those for the midline roofing elements. This produces a characteristic shape of the posterior third of the table, which is also seen in *Crassigyrinus* and early members of the Anthracosauria, notably the anthracosauroids.

4. The cranial dermal bones are almost unornamented. In this respect *Whatcheeria* differs strongly from colesteids and temnospondyls. We consider that the dermal ornament that is present most closely resembles that of anthracosaurs (see description and discussion in Panchen 1985, p. 551). Clack (in press) considers *Whatcheeria*'s ornament comparable to that of the anthracosauroid *Anthracosaurus russelli*. In view of the imprecision with which such a feature is necessarily described, *Whatcheeria*'s (weak) dermal ornament provides only suggestive evidence.

5. The orbits are large and quadrangular. This is also true of *Crassigyrinus* and early members of the Anthracosauria. Loxommatids have a markedly non-circular orbit as well, although in their case due to a large antorbital vacuity which is confluent with the orbit.

6. The vomers are narrow, even though they are primitive in retaining the fang-pair. Gauthier *et al.* (1988) consider narrow vomers to be a synapomorphy at their 'Node X', (Text-fig. 10) and note that it occurs in other anthracosaurs as well. Since 'broad' and 'narrow' are subjective, we consider this character to provide relatively weak support for the proposed relationship.

7. The maxilla has a marginal fang pair. On purely morphological grounds this could just as well be stated as 'Distinct caniniform maxillary tooth...present' (Gauthier *et al.* 1988, p. 125). The difference is subtle, but significant: traditionally, non-amniote early tetrapods have 'fangs', amniotes have 'canines'. Under either name, this feature is characteristic of early amniotes, as pointed out by Gauthier *et al.*, but not unique to them among early tetrapods; for instance, Dilkes (1990) has shown that Lower Permian trematopsid amphibians have two successive (presumably alternately replacing) caniniform teeth in each maxilla.

8. The interclavicle has a long parasternal process. This feature is characteristic of early amniotes, as pointed out by Gauthier *et al.* (1988), but is not unique to them among early tetrapods; for instance, *Ichthyostega* has a similar, though not as pronounced process (Jarvik 1980), as do some microsaur.

9. The scapulocoracoid possesses two ossification centres, one coracoid and one scapular. This is the earliest known appearance of this character, and in an otherwise very primitive animal. Panchen (*in* Panchen and Smithson 1988) cites this character as a synapomorphy of Seymouriamorpha, Diadectomorpha, and Amniota; it has not been described in Anthracosauroidea nor *Crassigyrinus*.

Characters 1–5 in the above list imply, if we have correctly interpreted polarities, a relationship between *Whatcheeria* and Anthracosauria as a whole. Characters 6–9 imply a relationship of *Whatcheeria* with some clade(s) included within Anthracosauria. *Whatcheeria* is not an anthracosaur, as it lacks the tabular-parietal contact that is usually considered one of that group's diagnostic characters. At the same time, *Whatcheeria* lacks such diagnostic characters of Panchen's Palaeostegalia (= *Crassigyrinus*) as minute forelimbs and a deep cheek below the orbits (cf. Panchen 1985). We suggest, therefore, that *Whatcheeria* be regarded for the present as the first outgroup to Anthracosauria, perhaps with *Crassigyrinus* as the outgroup to (*Whatcheeria* + Anthracosauria), as suggested by Bolt (1990).

Three features of *Whatcheeria* are so unexpected as to merit brief discussion in this preliminary description, even though we are uncertain of their implications.

1. We have found an intercentrum fused to its preceding pleurocentrum, as well as several examples of pleurocentral antimeres that are fused to one another dorsally. Fusion of the intercentrum to the preceding pleurocentra corresponds with Shishkin's (1989) 'anteropleural' pattern, of which he finds examples in a few temnospondyls. Pleurocentral fusion above the notochord but without midventral fusion is, so far as we are aware, not common in any other early



tetrapod, although fusion of pleurocentra only on the dorsal side is known to occur as 'occasional co-ossifications in old specimens' of *Eryops* (Moulton 1974, p. 25) and some other temnospondyls (Shishkin 1989). Even in those few temnospondyls where the pleurocentra are normally annular at some growth stage, available evidence indicates that fusion occurred first ventrally, then dorsally (*Doleserpeton*; Bolt 1969). Among anthracosaurs, as well, fusion of pleurocentra has long been considered to occur first ventrally, then dorsally. This opinion is based mainly on centrum morphology of anthracosauroids, particularly embolomeres. Holmes' (1984) description and discussion of pleurocentra in the embolomere *Proterogyrinus* is typical, and we have no reason to doubt his implied conclusion as to the likely ontogenetic sequence of fusion. If *Whatcheeria* really is related to Anthracosauria as we suggest, then its pattern of pleurocentral fusion is especially surprising. Perhaps, however, it should not be. For all practical purposes, the pleurocentrum is unknown in the other taxa that have been hypothesized to be immediate outgroups to Anthracosauria: the Palaeostegalia (*Crassigyrimus*) and the Loxommatoidea. The primitive condition of the anthracosauroid pleurocentrum is therefore uncertain, and it is not impossible that such a pleurocentrum would resemble that of *Whatcheeria*. However, it seems equally possible that other early tetrapods with 'normal rhachitinous' centra will turn out to have the condition found in *Whatcheeria*, if well-preserved specimens are examined with this in mind. At present, the usual assumption is that vertebrae that look 'rhachitinous' in lateral view will turn out to have unfused pleurocentra. But dorsally fused pleurocentra are not easy to recognize in articulated material, as we have found.

2. About half of the presacral ribs have uncinat processes. This is discussed by Bolt *et al.* (1988), and Bolt (1990). Such ribs are derived relative to osteolepiform fishes. Whether or not they are primitive for tetrapods as a whole, *Whatcheeria* provides the best evidence to date that they may have been primitive for anthracosaurs.

3. We have been unable to find a branchial skeleton in *Whatcheeria*, despite careful searching. This would normally be unremarkable, as it could be lost post-mortem even if present in life, which seems likely *a priori*. This is, after all, an animal that is manifestly aquatic based on morphology (e.g. lateral line canals) and circumstances of its occurrence. In the very primitive Devonian *Acanthostega*, moreover, ossified branchial arches are retained, apparently along with gill respiration (Coates and Clack 1991), and ossified branchial arches have been described in a number of temnospondyls.

In the case of *Whatcheeria*, however, we feel reasonably sure that an ossified branchial skeleton of primitive gill-bearing morphology was actually absent: we have not discovered it despite having at our disposal numerous articulated cranial remains, including several nearly complete skulls. Although the apparent absence of ossified branchial arches in *Whatcheeria* is unexpected, there is a parallel: Even the earliest representatives of Anthracosauria do not preserve ossified branchial arches as part of a (possible) gill-arch system. This is true even of aquatic species. Panchen (1970, p. 24) noted that 'no trace[s] of any post-hyoid branchial structures are recorded in anthracosaurs' (= Anthracosauroidea of Text-fig. 10). To the best of our knowledge, this is still the case. Where ossified branchial elements occur in anthracosaurs, it is as part of a hyoid apparatus that is greatly reduced and modified from the primitive condition seen in osteolepiform fish. These observations lead us to two tentative conclusions regarding the ecology and relationships of *Whatcheeria*: first, despite its primitiveness and apparent retention of a postbranchial lamina, *Whatcheeria* did not regain gill respiration; and second, the absence of ossified gill bars might be taken as an additional feature indicating relationship of *Whatcheeria* to anthracosaurs.

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